Pergamon

0042-6989(95)00033-X

Vision Res. Vol. 35, No. 23/24, pp. 3243–3254, 1995

0042-6989/95 $9.50 + 0.00

Rotation of Listing's Plane by Horizontal, Vertical and Oblique Prism-induced Vergence

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Received 27 October 1994; in revised form 31 January 1995

We examined the changes in Listing's plane resulting from prismatically induced vergence. The three-dimensional angular positions of the two eyes were compared in normal subjects wearing search coils and gazing at targets 1.9 m away with and without prisms. For horizontal base-out prisms each degree of convergence in one eye yielded 0.72 deg of temporal rotation of Listing's plane in that eye. The results from vertical prisms were not what was expected from the horizontal results. A base-up prism on the right eye induced a downward and temporal rotation of Listing's plane. A base-down prism on the right eye induced an upward and nasal rotation of Listing's plane. The effects of oblique prisms were those expected from combining the effects of horizontal and vertical prisms. Thus in addition to producing a horizontal or vertical misalignment of the gaze line, prisms induce an unexpected position-dependent torsional disparity.

Three-dimensional eye movements   Listing's law   Vergence   Prisms   Torsional disparity   Human

INTRODUCTION

Convergence of the two eyes on a near object produces a torsional change in angular eye position (Allen, 1954; Mok, Ro, Cadera, Crawford & Vilis, 1992; Van Rijn & Van den Berg, 1993; Van Gisbergen & Minken, 1995; Minken & Van Gisbergen, 1994). If one saccades between several targets while maintaining a constant vergence, i.e. directing gaze over an isovergence surface, eye position remains confined to Listing's plane but Listing's plane is rotated temporally. This rotation is directly dependent on the amount of vergence. Because of this rotation of Listing's plane, torsion becomes dependent on gaze direction (Mok *et al.*, 1992). The eyes show progressively more extorsion as they look down and progressively more intorsion as they look up.

Simple prisms, depending on their orientation, produce horizontal or vertical displacements of an image. They do not, on their own, rotate an image torsionally. However when different prisms, or identical prisms with different orientations, are placed over the two eyes, the images can be fused through the action of the vergence system. The first goal of this study was to determine if this prism-induced vergence produced a rotation of Listing's plane similar to that observed when viewing near objects. The results show that base-out prisms induce convergence which in turn produces a temporal or outward rotation of Listing's plane in the two eyes very similar to that observed when subjects converge on an isovergence surface (Mok *et al.*, 1992).

The second goal was to determine if vertical prism-induced vergence shows a similar effect. If so, one would expect Listing's plane to turn in the opposite direction to vertical vergence; that is if the prism caused vergence to rotate the eye up, Listing's plane should rotate down. However Straumann and Müller (1994) have observed a surprising horizontal (i.e. about a vertical axis) rotation of Listing's plane when subjects fuse through vertical prisms. The prisms used were very weak, 0.75 D in opposite directions on each eye. To reexamine this effect we trained subjects to fuse through stronger vertical prisms. Finally, we examined Listing's plane while subjects fused through an obliquely oriented prism to determine whether this produced a combination of the rotations observed using horizontal or vertical prisms alone.

METHODS

The results were obtained from normal human subjects none of whom had ocular pathologies other than a mild refractive error. Three-dimensional eye and head orientations were sampled at 100 Hz using Skalar search-coils (Collewijn, Van der Mark & Jansen, 1975) placed in each eye and on the forehead. The subject's head was centered within three orthogonal magnetic fields generated by Helmholtz coils, 1 m square, and was not restrained. The head was not physically restrained so that we could determine where the subjects placed Listing's

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plane in the normal state (see Fig. 4). The subjects were asked to look at the central target at the beginning of the trial and then to hold the head still while saccading between targets. All subjects complied and only small (<2 deg) head movements were observed. The effects of these small head movements were eliminated by using the head position to compute the eye position relative to the head (see later). Subjects were asked to look at a center target in the sagittal plane, at eye level 1.9 m away. The positions of the two eyes and the head recorded at this moment were defined as their reference positions. A photograph of the subject's head was taken from the side to correlate these reference positions to anatomical landmarks.

To compute the location of Listing's plane, subjects saccaded between nine targets in a 3 × 3 square array spanning ±15 deg horizontally and vertically. All nine targets were continuously visible, as were a variety of interspersed colored photographs and shapes used to assist in fusion. During this task the subject held the head still. The position of the eye relative to the head, q_{eh}, was computed using the quaternion product

$$q_{eh} = q_{hs}^{-1} q_{es}$$

where q_{es} is the quaternion representation of eye orientation (Westheimer, 1957) relative to space (the field coils) as described by Tweed, Cadera and Vilis (1990) and q_{hs} is the same for the head. We recorded 50 sec of data (approx. 100 saccades, sampling rate 100 Hz) under control conditions and an equal period of time while the subjects wore prisms and viewed the same nine targets. The eye positions just prior to each saccade were fitted to a plane, the displacement plane, which defined eye positions relative to the center reference position (Tweed *et al.*, 1990). A normal to this plane bisects the angle between reference gaze direction and the primary gaze direction. Listing's plane is, by definition, perpendicular to the primary gaze direction. The rotation of Listing's plane was then compared to the change in vergence as measured by the average horizontal and vertical angles between the gaze directions of the two eyes, (right − left eye gaze direction with prisms) − (right − left eye gaze direction without prisms).

Horizontal and vertical prism-induced vergence was produced by Fresnel lenses attached to plastic spectacle frames with the opposite orientation for each eye. The effect of oblique prism-induced vergence was measured using loose plastic prisms hand held obliquely at 45 deg by the subject over one eye and oriented base-out and up, or base-out and down. Subjects had great difficulty fusing targets while wearing vertical prisms and somewhat less trouble with oblique prisms. To facilitate fusion we started with weak prisms on each eye and gradually increased these in 1 D steps over 30–60 min to the maximum strength at which the subject could learn to fuse. The search coils were then inserted and eye movements recorded while the subject wore prisms. The prisms were then removed and subjects then viewed the targets until fusion was reestablished, usually after 5–10 min. Control values were recorded. Subjects were then given a shorter training regimen, lasting about 15 min with the prisms reversed, followed by another control. This second training regimen was shorter because we limited the total recording time to 30 min.

RESULTS

Horizontal prisms

The effect of vergence through base-out prisms on Listings plane was very similar to that reported by Mok *et al.* (1992) during convergence on near targets. Figure 1 shows the angular positions of the two eyes when gaze is directed at the nine distant targets, ±15 deg horizontal and vertical. These positions are viewed from above to show the planar nature of the data. The middle row shows eye positions when viewing the same targets through 30 D base-out prisms on both eyes. A small outward or temporal rotation of the data is seen. Thus the torsional orientation of the eye relative to the head changes depending on the position of the eye: when the eyes look down, the left eye is rotated more counterclockwise; while the right eye is more clockwise. In other words, while looking down the two eyes became more excyclorotated.

To quantify these changes in eye position, the data were fitted to a plane: the displacement plane (Tweed *et al.*, 1990). These fitted planes are viewed from above in Fig. 2. In the left eye this plane is parallel to the horizontal axis under control conditions and becomes rotated temporally when the subject wears prisms. In the right eye the plane is rotated slightly nasally under control condition and again rotates temporally with prisms.

From these fitted displacement planes, Listing's plane was computed. Primary gaze direction is perpendicular to Listing's plane. As derived by Tweed *et al.* (1990), Listing's plane rotates twice as much as the displacement plane and thus primary gaze direction (labeled *P* in Fig. 2) rotates twice as much as the perpendicular to the fitted plane (dashed line in Fig. 2).

Figure 2 shows that primary gaze direction is not the same in the two eyes under control conditions. The fact that it is not symmetrical is possibly due to small misalignment of the head's sagittal plane. Presumably in this case, the head was turned slightly to the left at the start of the experiment rather than the assumed forward pointing direction. The average difference between the primary gaze directions of the two eyes under control conditions varied in the five subjects from converging by 5.5 deg to diverging by 9.8 deg (Fig. 3), mean 1.2 deg converging ±6.4 deg SD. Vertically the differences between the two eyes were somewhat smaller and less variable, mean 0.9 ± 1.9 deg. Since the subjects were free to move their heads, they were able to reposition primary gaze direction relative to the targets at the start of each test period. As shown by Fig. 4, subjects positioned the average vertical primary gaze direction of the two eyes remarkably close to the direction of the central target, mean 2.1 ± 2.7 deg. This direction was 21 ± 6 deg below a line connecting the external auditory meatus and the center of the pupil.

The effects of prism-induced vergence were quantified by measuring the change in the orientation of Listing's plane for each prism-induced change in vergence. Prisms of 10, 20 and, if tolerated, 30 D were placed base-out on each eye. On average, the eyes verged by a factor 0.86 ± 0.09 SD of that required by the prisms. The mean convergence for the nine targets was computed. This mean was fairly constant (SD $\pm$ 1.5 deg) for prisms of 10 and 20 D rising slightly (SD $\pm$ 3 deg) for 30 D prisms. Figure 5 shows that this convergence produced a temporal rotation of Listing's plane. A least squares estimate of the straight line fit to the data indicated that on average a 1 deg change in vergence produced a 0.72 deg rotation of Listing's plane (see Table 1). These base-out prisms produced no consistent up/down rotation of Listing's plane (Table 1).

Figure 1 also shows that prism-induced vergence, in addition to turning Listing's plane, also produced a small shift of Listing's plane, pushing the plane of the left eye back (i.e. in a counterclockwise direction) and that of the right eye in a clockwise direction. Thus convergence appears to produce a small extorsion in the two eyes. All subjects showed a similar change, producing on average 0.1 deg $\pm$ 0.02 SD of extorsion per degree of vergence. A similar shift has been observed when subjects converged on closed targets (Minken & Van Gisbergen, 1994) but not when subjects viewed targets on an isovergence surface (Mok *et al.*, 1992).

Lastly, the above views in Fig. 1 suggest that Listing's plane has a thickness. This thickness of Listing's plane was estimated by computing the SDs of the scatter about the fitted plane in the torsional direction. For the five subjects, the average thickness in the control condition was ± 0.63 deg for the left eye and ± 0.64 deg for the right. (These values were lower than previously observed in this laboratory, possibly because the range of eccentricities over which Listing's plane was measured, $\pm$ 15 deg, was smaller than in these previous studies.) The thickness of the plane increased very slightly during prism-induced vergence to 0.68 deg in the left eye and 0.69 deg in the right eye.

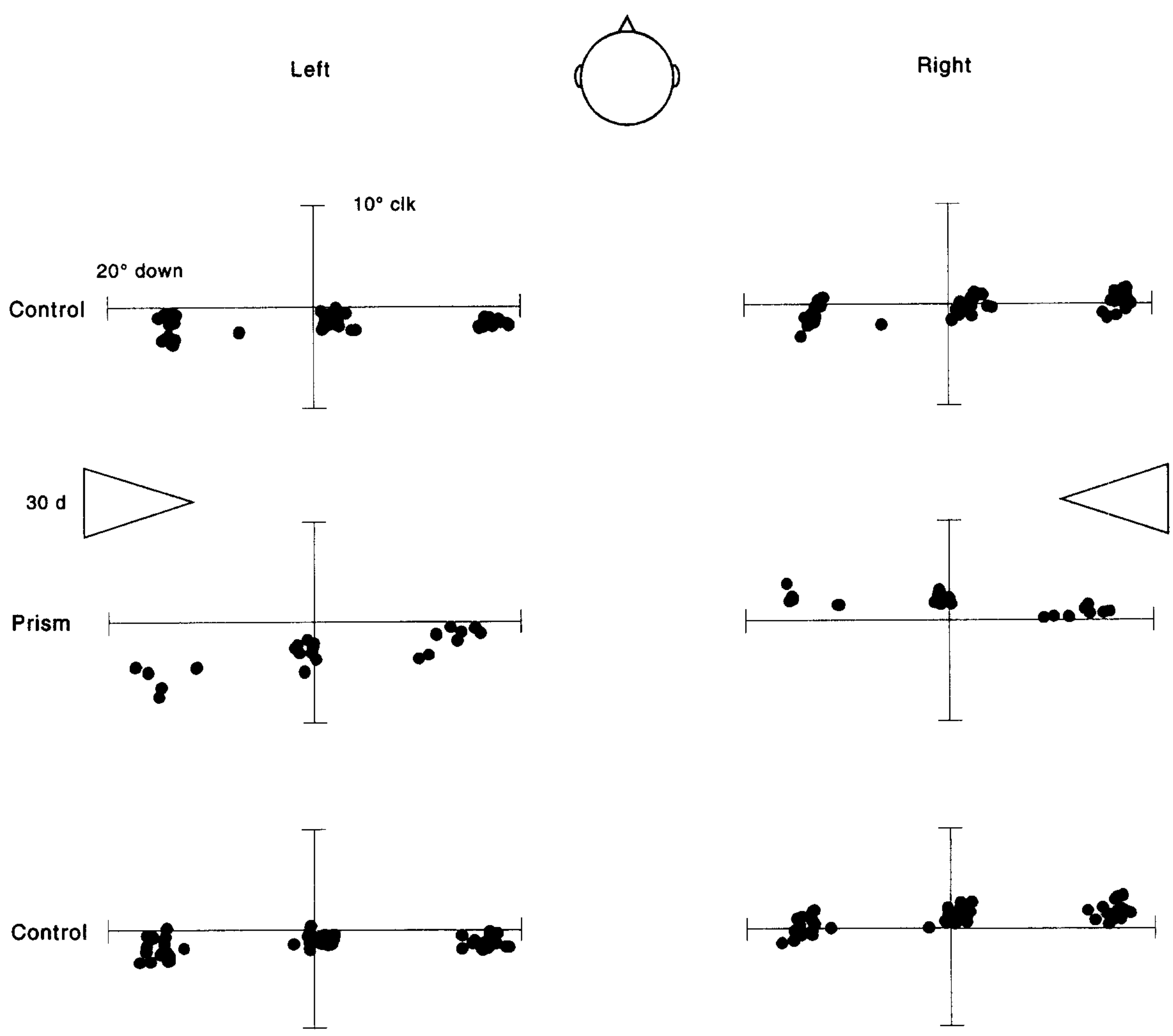

FIGURE 1. Angular position of the left and right eyes when fixating distant targets. Each dot indicates the three dimensional eye position as viewed from above the subject with the nose pointing to the top of the page. The top and bottom control rows indicate the positions when fixating the nine targets directly. The middle row shows the positions while viewing the same targets through 30 D base-out prisms on both the right and left eyes. clk, clockwise with respect to the subject. Subject PE.

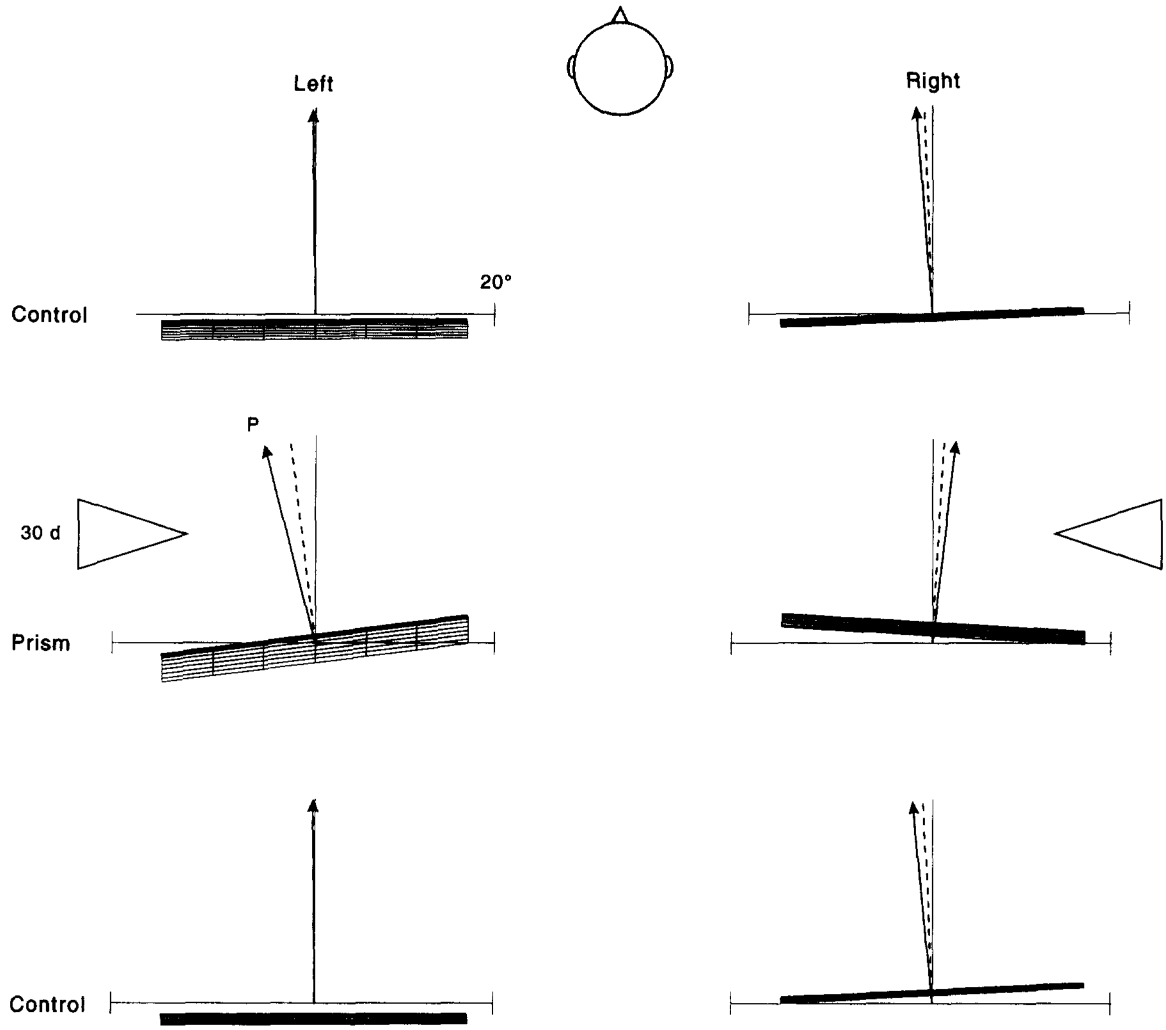

FIGURE 2. A plane fitted to the data shown in Fig. 1 as viewed from above. The dark line on the plane indicates its top edge. The arrow marked *P* is the computed primary gaze direction.

Vertical prisms

The effects of vertical, prism-induced, vergence was examined by placing a vertically oriented (e.g. base-up) prism on the right eye and the reverse on the left (e.g. base-down). As described in the Methods, the subjects were trained with prisms of gradually increasing diopters. Despite this graduated build up, few subjects could overcome more than 3 or 4 D on each eye. We examined the changes in Listing's plane in the five of seven subjects who elicited the largest vertical vergence response (Fig. 6). The maximum prisms in these subjects were 7, 5, 4, 3 and 1.5 D on each eye. In these five subjects, the actual vergence was 0.61 ± 0.22 SD of that expected from the prisms, less than in the horizontal case. Reversing the prisms (base-down on right eye and base-up on the left) elicited a smaller vergence effect here because, as indicated in the Methods, the training regimen was shorter.

Compared to the horizontal prism results, several additional differences were noted. First, vertical vergence appeared to produce an up/down rotation of Listing's plane [Fig. 6(A)]. On average, for every degree of vertical vergence, Listing's plane turned by 1.34 deg ± 0.23 SE ($r^2 = 0.61$). The direction of the turn was opposite to that seen with horizontal prisms. Here, with a base-up prism over the right eye, the right eye verged down and Listing's plane and primary position also on average rotated down [Fig. 7(B)]. By comparison, in the horizontal case, as vergence turned the eye inward, Listing's plane and the primary gaze direction turned outward [Fig. 7(A)]. The slope here was more variable across subjects (thin lines Fig. 6) than with horizontal prisms. This is reflected in the larger SE (Table 1). One subject, TV, verged by 7 deg and produced a large turn of Listing's plane while another, DN, verged little and exhibited almost no turn. This greater variability may be due to the small vertical vergence that could be elicited thus making this measure more susceptible to noise.

Vertical prisms also appeared to elicit a horizontal rotation of Listing's plane. Listing's plane turned outward when base-up prisms were placed over the right eye (and with base-down prisms over the left) and it turned inward when the prism were reversed, slope 0.81 [Fig. 6(B)]. This horizontal rotation was correlated with the vertical change in vergence ($P < 0.002$, Table 1) and not with a small horizontal change in vergence ($P > 0.5$).

Finally, Enright (1992) and Van Rijn and Collewijn (1994) have reported a conjugate counterclockwise rotation of the eyes during vertical vergence (left eye above right eye). Here the fitted planes of both eyes did on average shift slightly in the counterclockwise direction with base-up prisms on the right eye and the opposite with base-down. However this shift was variable and not statistically significant (slope shift/vergence: left eye, 0.18, $r^2 = 0.17$; right eye, 0.03, $r^2 = 0.19$).

Oblique prisms

A prism with the base angled 45 deg up and right, or 45 deg down and right, was placed over the right eye of five subjects. These prisms induced an oblique vergence response. Assuming that the expected response in each component was $1/\sqrt{2}$ the strength of the prism, the actual average gain was 0.52 ± 0.11 SD horizontal and 0.42 ± 0.09 SD vertical, less than with either the horizontal or vertical prisms alone.

As expected, both vertical and horizontal rotations of Listing's plane were observed. The relationship between the vertical component of vergence and the vertical rotation of Listing's plane was similar to that observed with vertical prisms [Fig. 8(A)]; the rotation of Listing's plane was in the same direction as the rotation of the eye due pure vertical prisms but somewhat smaller, 0.62 ($r^2 = 0.73$, Table 1).

The horizontal rotation of Listing's plane was different

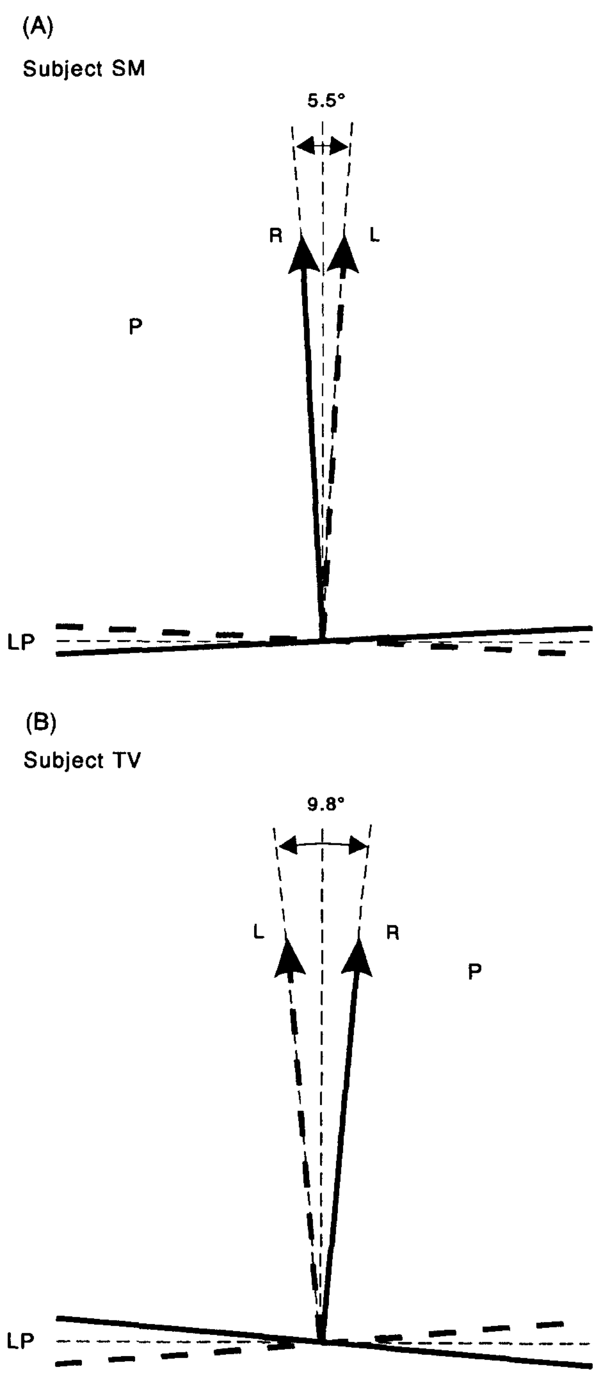

FIGURE 3. The above view of the primary gaze direction when viewing the distance targets with no prisms. The subject with the most nasal pointing direction is shown in (A) and the subject with the most temporal in (B).

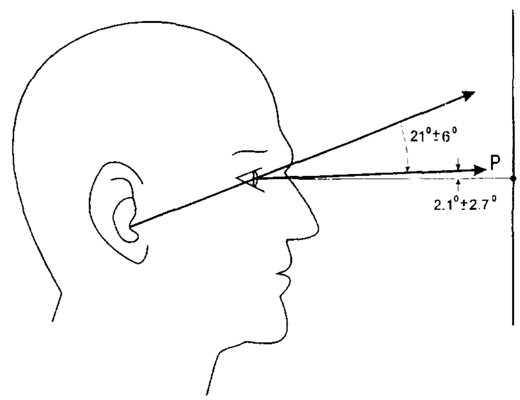

FIGURE 4. The average primary gaze direction in relation to anatomical landmarks on the head, i.e. a line drawn from the external auditory meatus through the center of the globe.

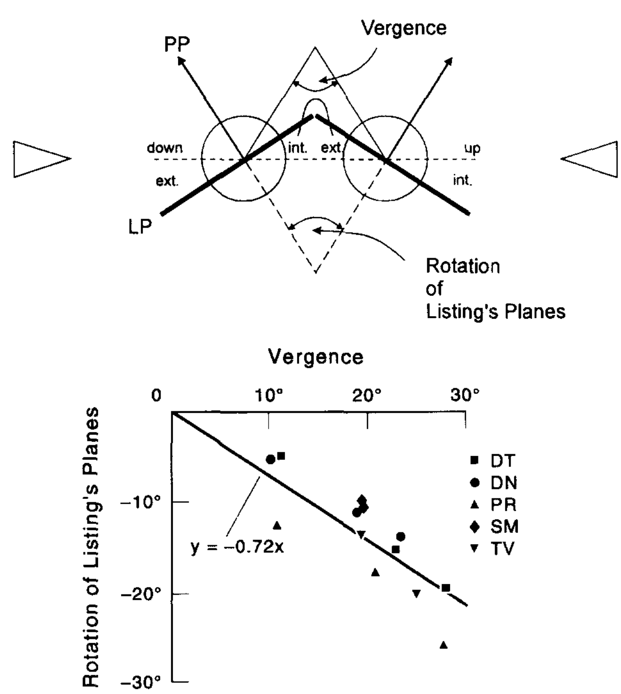

FIGURE 5. The combined rotation of Listing's plane in the two eyes as a function of change in the horizontal vergence (with prisms minus without prisms) in five subjects. Vergence was induced by base-out prisms of 10, 20, and, if capable of maintained fusion, 30 D over each eye. The line is the least squares estimate of the straight line fit to the data.

TABLE 1. Least squares estimate of the relation between the rotation of Listing's plane and the vergence induced by horizontal (base-out) prisms, vertical (base-up or base-down) or oblique (base 45 deg up or down and out)

	Vergence	Rotation of Listing's plane	y Intercept = 0		
			Slope ± SE	r^2	P
Horizontal prism					
	Horizontal	Horizontal	-0.72 ± 0.04	0.69	< 0.001
	Horizontal	Vertical	0.13 ± 0.05	0.05	> 0.5
Vertical prism					
	Vertical	Vertical	1.34 ± 0.23	0.61	< 0.001
	Vertical	Horizontal	0.81 ± 0.21	0.35	< 0.002
	Horizontal	Horizontal	1.86 ± 0.97	-0.01	> 0.5
Oblique prism					
	Vertical	Vertical	0.62 ± 0.11	0.63	< 0.001
	Vertical	Horizontal	0.84 ± 0.20	0.29	< 0.001
Base-up oblique prism					
	Horizontal	Horizontal	-1.00 ± 0.16	0.44	< 0.05
Base-down oblique prism					
	Horizontal	Horizontal	0.09 ± 0.14	-0.01	> 0.5

Based on all the subjects shown in Figs 5–7.

depending on whether the prism was angled up and right [Fig. 8(B)], or down and right [Fig. 8(C)], over the right eye. For the prism angled up and right, the slope for horizontal rotation of Listing's plane for a horizontal change in vergence was -1.0 ($r^2 = 0.44$). This was somewhat higher than that for horizontal or vertical prisms alone. Presumably this was due to an additive effect; the horizontal component of the prism induced a horizontal temporal rotation of Listing's plane as did the vertical [Fig. 9(A)]. For the prism angled down and right,

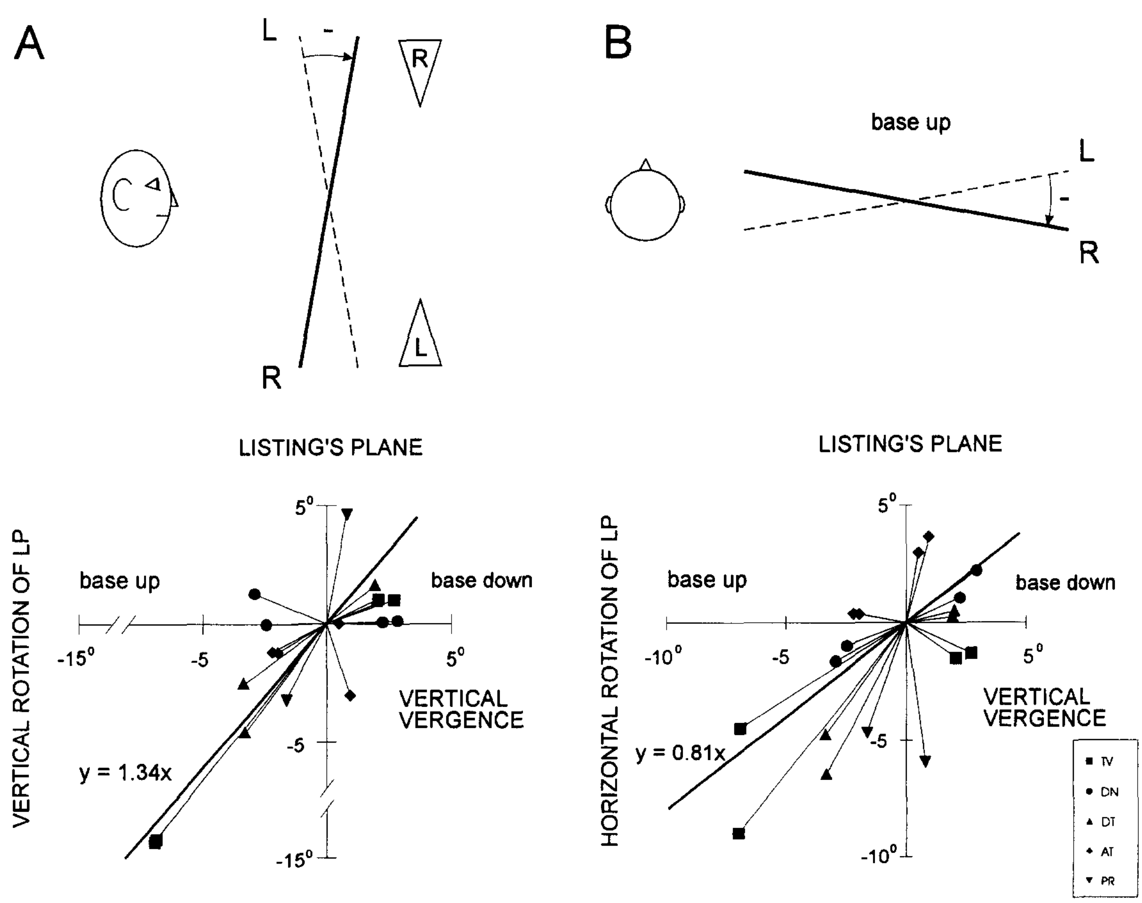

FIGURE 6. The combined rotation of Listing's plane in the two eyes as a function of vertical vergence in five subjects. (A) Rotation of Listing's plane about the horizontal axis. Negative rotation defined as the right eye's Listing's plane being tilted forward relative to that of the left. (B) Rotation of Listing's plane about the vertical axis. Negative rotation of Listing's plane is defined as the right eye's plane being turned to the right of that of the left eye. Negative vertical vergence is that produced by a base-up prism on the right eye and a base-down on the left. Positive vergence is produced when the direction of the prisms is reversed. Symbols with thin lines indicate the average change in vergence and the rotation of Listing's plane relative to the no prism control condition for each subject.

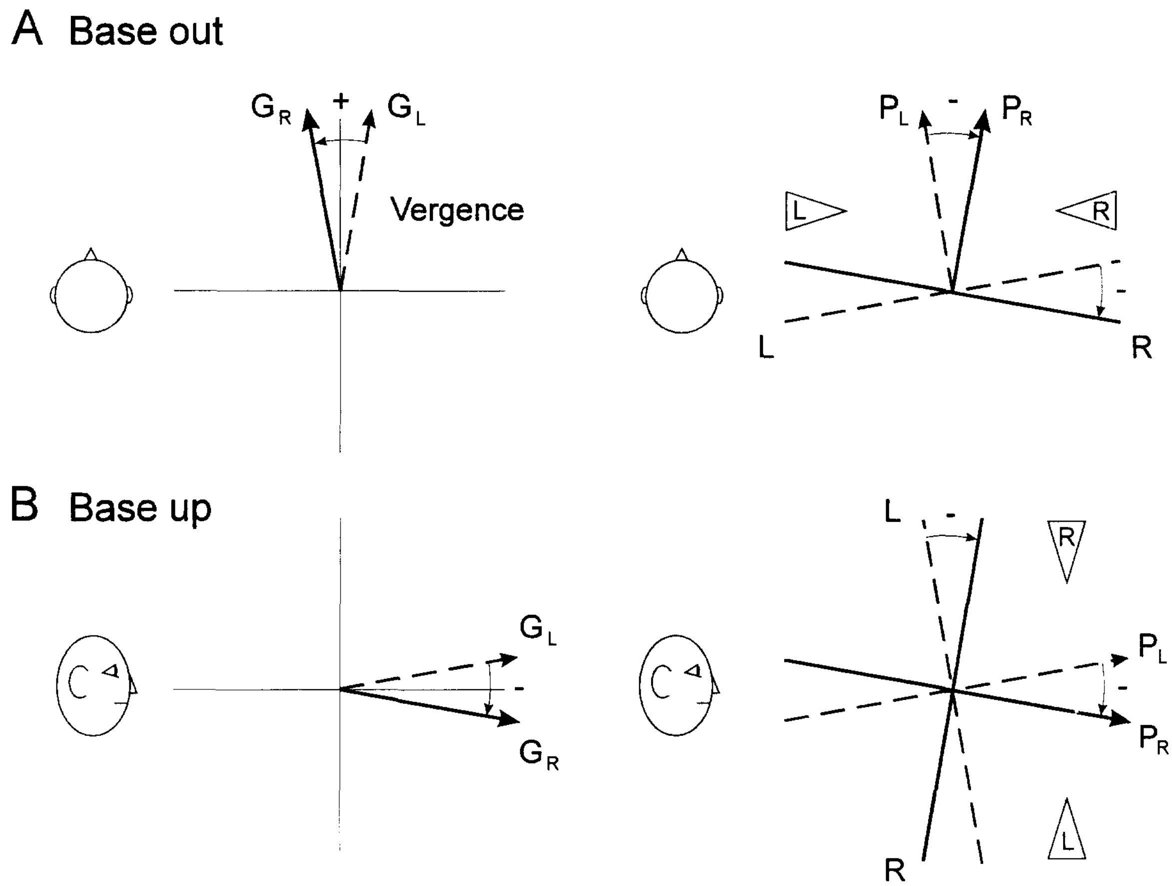

FIGURE 7. Comparison of the effects of horizontal base-out prisms (A) and vertical prisms (B), base-up on the right eye and base-down on the left eye on Listing's plane. The arrows labeled + or − indicate the sign convention used to denote vergence and the rotation of Listing's plane in Fig. 6. Left: gaze direction G_r right eye (solid line), G_l left eye (dashed line). Right: Listing's plane and primary direction (P).

the slope was small, 0.09 [Fig. 8(C)] and not significantly different from zero (Table 1). Presumably this was also due to an additive effect, in this case resulting in a cancellation. The horizontal component of the prism should, as always, produce a temporal rotation of Listing's plane but the vertical component should now produce a nasal rotation [Fig. 9(B)]. Thus the rotations observed with oblique prisms are consistent with those from horizontal and vertical prisms.

DISCUSSION

Horizontal prisms

Prism-induced vergence appears to alter the orientation of Listing's plane relative to the head. Because the primary gaze position is perpendicular to Listing's plane, prisms alter its direction as well. This reorientation is dependent on the amount of prism-induced vergence. Thus it is perhaps not surprising that the reorientation of Listing's plane is very similar to that induced when verging on actual near targets. Mok *et al.* (1992) observed a mean temporal rotation of 9.2 deg in the right eye and 9.8 deg in the left eye when fixating targets on a surface that required 30 deg of combined convergence in the two eyes. This translates into a slope of 0.63 [(9.2 + 9.8)/30]. Since the actual vergence was on the average 0.96 of the required, this raises the slope slightly to 0.66. Here, in the case of base-out prisms, Listing's plane rotated by 0.72 deg for every degree of actual convergence, a value close to that reported earlier.

What is the functional significance of the temporal rotation of Listing's plane? Suppose that primary gaze direction [P in Fig. 10(A)] was directly forward in both eyes. Then saccades, between distant vertically displaced targets, would rotate the eyes about the axes in Listing's plane. These rotations in Listing's plane are optimal in that these are the shortest rotations between the two vertically displaced gaze directions. Suppose now these targets are 30 deg to the right [Fig. 10(B)]. Listing's law requires that the velocity axes of these saccades rotate out of Listing's plane in the same direction as G, the gaze direction, but by half the amount (Tweed & Vilis, 1990). Rotations about these axes are not optimal, i.e. they are larger than in Fig. 10(A). For targets 30 deg to the left the reverse happens [Fig. 10(C)]. Suppose that one could verge 30 deg in each eye and this vergence had no effect on Listing's plane. Then the axes of saccades between near vertically displaced targets directly in front of the subject would have the same axes as in Fig. 10(B) in the left eye and Fig. 10(C) in the right eye; both rotated nasally and neither optimal for these vertical rotations. Suppose instead Listing's plane were to rotated by as much as vergence, but in the opposite direction [Fig. 10(D)]. In this case ω remains in the same position as for distant forward targets, in the frontal plane and optimal for a forward pointing gaze direction, G'. Thus when vergence resets the location of Listing's plane, eyes respond as if the fovea had been directed toward a forward G', not the actual nasal G, target. By doing so, saccades to and from targets directly in front of the head remain optimized. A mathematical implementation of this fovea resetting model was detailed in Mok *et al.* (1992).

The temporal rotation of Listing's plane has been confirmed in two recent studies (Van Rijn & Van den Berg, 1993; Minken & Van Gisbergen, 1994). However, quantitatively there are some differences. A comparison of these differences is somewhat difficult because this reorientation of Listing's plane was expressed differently. Suppose for the sake of illustration that our results had shown the optimal gain of 1.0, i.e. for every 2 deg of convergence (1 deg in each eye) there was a 1 deg temporal rotation of each eye's Listing's plane. Then as each eye turned nasally 15 deg during convergence (Fig. 11), each eye's Listing's plane and primary gaze direction would rotate temporally by 15 deg. To compare the torsion in the two eyes we must consider a common reference which in turn requires a comparison of the displacement planes. Displacement planes rotate half as far as Listing's plane, 7.5 deg (Fig. 11). Now when the eyes look 30 deg up, the change in torsional component of the left eye is

$$\Delta r_{t1} = e\tan(\Delta v/4) = 0.26 \times 0.13 = 0.034 = \sin(\alpha/2)$$

then $\alpha \approx 4$ deg where e is $\sin(30°/2)$ if the scale is in quaternion vectors (Tweed *et al.*, 1990), or $\tan(30°/2)$ if in rotation vectors (Haustein, 1989). Our actual measured gain was 0.72 of this.

Minken and Van Gisbergen (1994) quantified their results in terms of the change in normalized cyclotorsion as a function of eye elevation, i.e. $[(\Delta g_1/\Delta V)/E]$ = [(change in torsion in the two eyes)/(change in vergence in the two eyes)]/elevation. Each angle was expressed in terms of rotation vectors. The change in torsion between the two eyes is not simply 2×4 deg or 8 deg, but about twice that, 16 deg. This is because, as pointed out by Minken, Gielen and Van Gisbergen (1995), the relative position of the two eyes is the amount of rotation required to take the left eye to the right eye, $g = r_r r_l^{-1}$. The expected value of the torsional component of this rotation is

$$\Delta g_1 = 2E\Delta V = 2\tan(30°/2)\tan(30°/2)$$
$$= 2(0.27 \times 0.27) = 0.14 = \tan(\alpha/2)$$

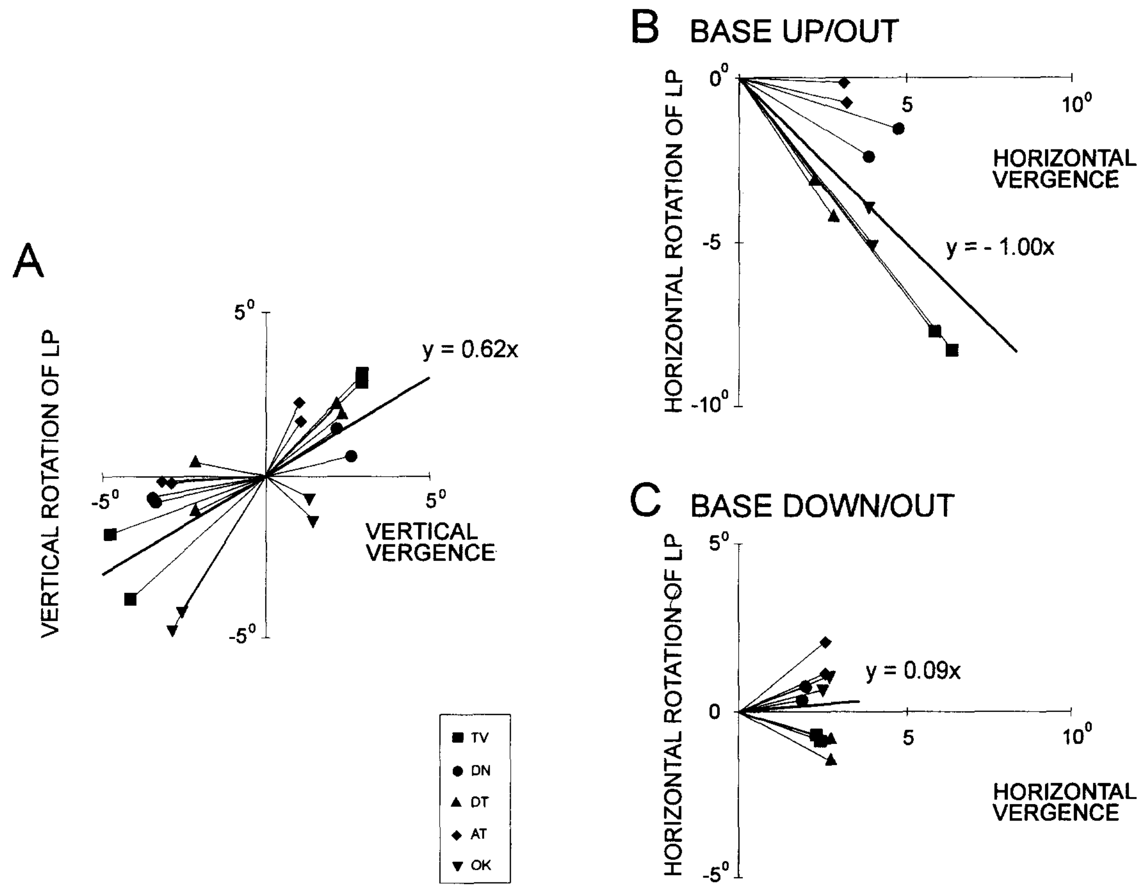

FIGURE 8. The rotation of Listing's plane in the two eyes as a function of oblique vergence in five subjects. (A) Rotation of Listing's plane about the horizontal axis (vertical rotation) as a function of vertical component of vergence produced by oblique prisms over the right eye (base-up-and-out or base-down-and-out). (B) Rotation of Listing's plane about the vertical axis (horizontal rotation) as a function of the horizontal component of vergence produced by base-up-and-out prism over the right eye. (C) Same as (B) except that a base-down-and-out prism is used. Symbols with thin lines indicate the average change in vergence and the rotation of Listing's plane relative to the no prism control condition for each subject.

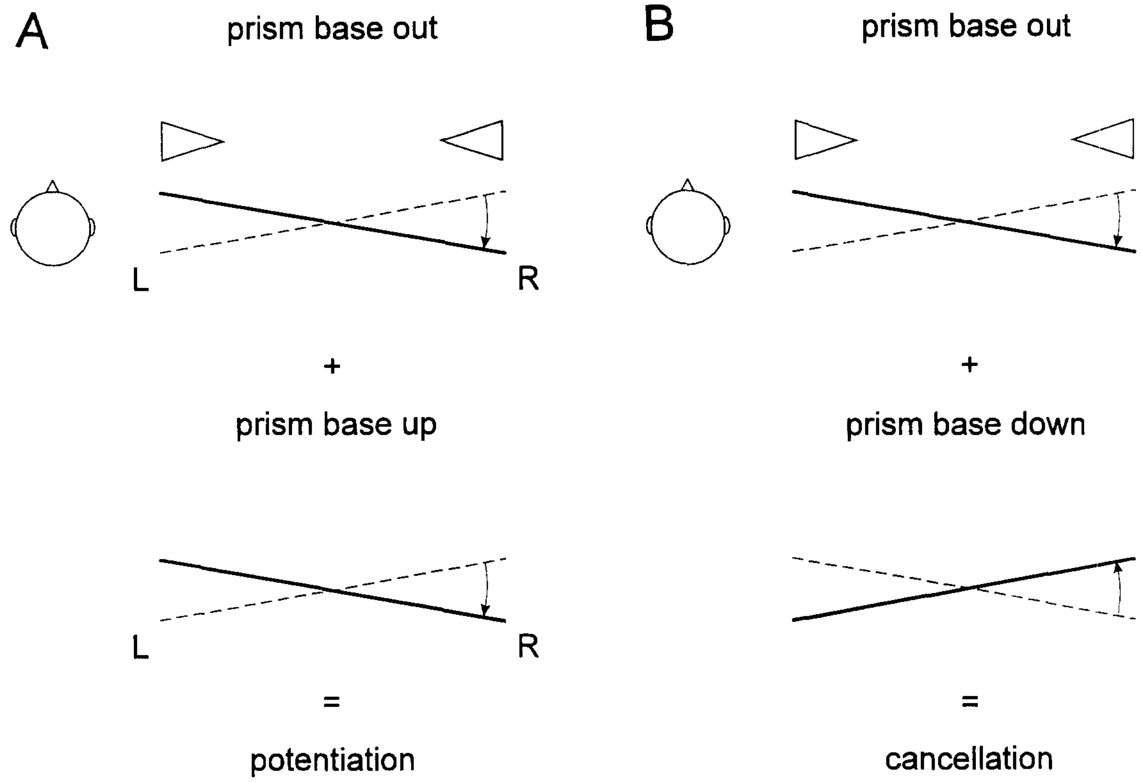

FIGURE 9. An explanation of the potentiation and cancellation observed with oblique prisms in Fig. 8(B, C). (A) The base-up component of the prism produces a temporal rotation of Listing's plane which potentiates the effect of the base-out component. (B) The base-down component of the prism produces a nasal rotation of Listing's plane which cancels the effect of the base-out component.

then $\alpha \approx 16$ deg. Their expected $\Delta r_{\ell 1}$ works out to be about 4 deg, the same as ours. The authors observed $2.15/2 = 1.08$ of this.

Van Rijn and Van den Berg (1993), using Helmholtz angles for elevation and vergence, predicted that the left eye's torsion should change by

$$r_{\ell 1} = \frac{EV}{4} = \left(\frac{\pi}{2}30^\circ\right)\left(\frac{\pi}{2}30^\circ\right)4$$

$$= \left(\frac{0.52 \times 0.52}{4}\right) = 0.7 = \tan(\alpha/2)$$

then $\alpha \approx 8$ deg. Their expected values are twice as large as those of Minken and Van Gisbergen (1994) and ours because their model was based on a difference vector scheme, rather than the rotation vector scheme (Minken *et al.*, 1995). Van Rijn and Van den Berg (1993) observed 0.855 of their expected value.

In summary, the comparable values of the actual observed $r_{\ell 1}$ listed in the order shown above are $0.72 \times 4 = 2.9$ deg, $1.08 \times 4 = 4.3$ deg, 0.855×8 deg $= 6.8$ deg. Thus while our results indicate less torsion than either of these studies they are much closer to those reported by Minken and Van Gisbergen (1994). What might be the reasons for these observed differences?

It may be that the rotation of Listing's plane induces a torsional disparity. Rogers and Howard (1991) and Van Rijn, Van der Steen and Collewijn (1994) have shown that visual torsional disparity induces a compensatory motor cyclofusion. This in turn may reduce the temporal rotation of Listing's plane. As detailed in the Methods, the peripheral visual information was extensive in our case, moderate in Minken and Van Gisbergen (1994) and least in Van Rijn and Van den Berg (1993), suggestive of an inverse relation to the gain of the observed torsion. However Minken and Van Gisbergen (1994) showed that reducing the amount of visual information did not increase the effect they observed. Thus this does not explain the comparatively large values observed by Van Rijn and Van den Berg (1993). However, increasing the amount of visual information may explain our lower values.

On the other hand, Van Rijn and Van den Berg (1993) may have overestimated the observed torsion. Their estimate was base on the slope of the relation between $r_{\ell 1}$ and $EV/4$, pooled for all fixation conditions. For far fixation distances, the vergence V decreases to zero. However in this case Listing's plane may have a small nasal or temporal rotation, as observed here (Fig. 3). which would produce a finite $r_{\ell 1}$ when the eye is elevated or depressed. This would result in a very large slope, raising the averaged slope of the pooled data.

Vertical prisms

The effects of vertical prisms are somewhat more variable than those of horizontal prisms. This variability is perhaps not surprising considering that, in the case of vertical prisms, we are dealing with very small changes. On average our subjects could not fuse vertically, even with practice, more than 3 or 4 prism D on each eye. This is almost an order of magnitude less than their capacity with base-out prisms (presumably because vertical prisms produce a more unnatural visual experience). For 2 prism D on each eye, Listing's plane rotates by roughly 1 deg and this is measured by a rotation of the displacement planes of roughly 0.5 deg. These displacement planes are measure by fitting a plane to the actual eye position. The torsional variability of eye position is on the average 0.6 deg; a value which is small with respect to the ± 15 deg horizontal and vertical changes in eye position but large with respect to the rotations of the displacement planes.

The effects of vertical prism observed here are somewhat different from those observed previously by Straumann and Müller (1994). In their experiments, weaker prisms produced an inward or nasal rotation of Listing's plane rather than the outward or temporal rotation observed here. In addition their experiments showed no consistent tilt about the horizontal axis. Straumann and Müller (1994) measured the change in the orientation of Listing's plane between monocular and binocular conditions, both with and without prisms [i.e. (mono − bino) − ($mono_{prism}$ − $bino_{prism}$) whereas we measured ($bino_{prism}$ − bino)]. It is possible that phorias appeared during monocular viewing and these phorias themselves may have caused Listing's plane to tilt, obscuring the direct effect of the prisms. The other possibility is that the immediate effect of prisms is different from that observed after some training.

The effects of vertical prisms observed here are also different from those observed with horizontal prisms. In the case of horizontal prisms, the vergence induced gaze shift (nasal) and rotation of primary gaze (temporal) are in opposite directions. This results in a conjugate extorsion when looking down and a conjugate intorsion

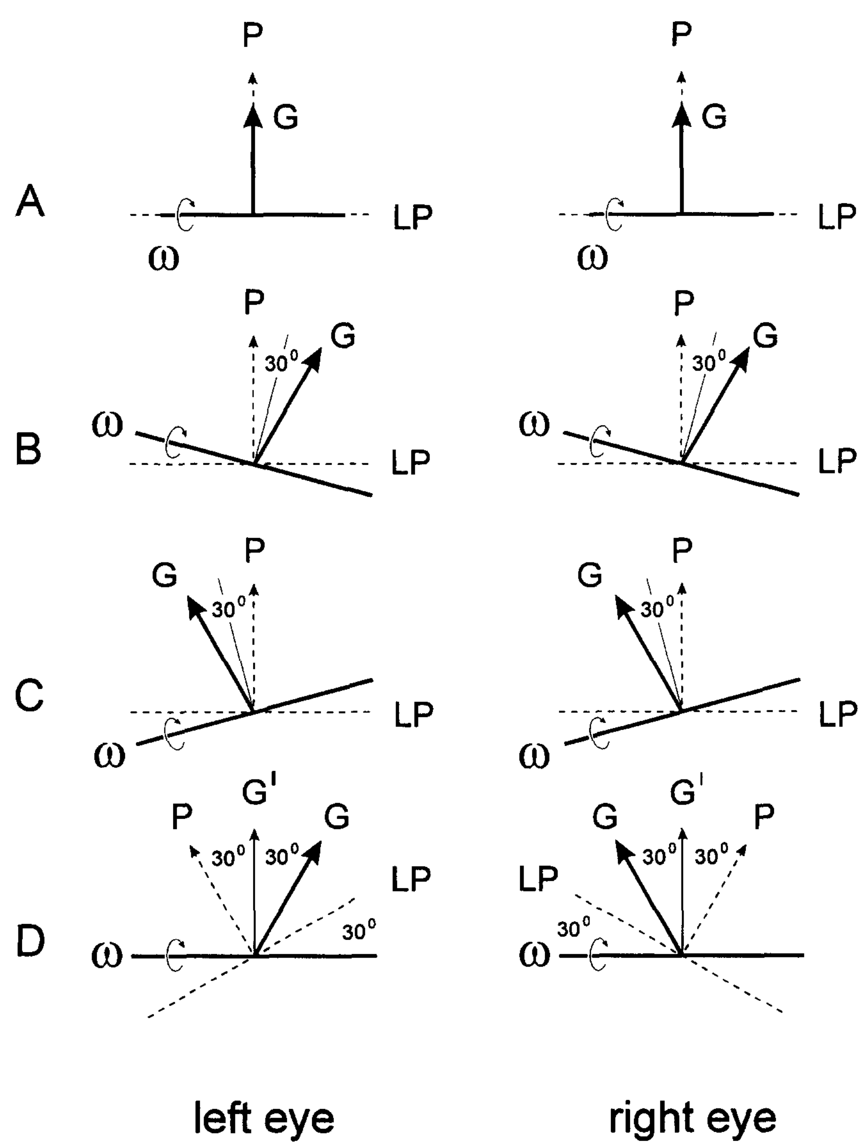

FIGURE 10. The functional significance of Listing's plane rotation during convergence. (A) During saccades between distant vertically displaced targets in the direction *G*, the axes of rotation (ω) are optimal and in Listing's plane (LP). (B) The axes of saccades between vertically displaced targets 30 deg to the right are not optimal. (C) The same for targets displaced 30 deg to the left. (D) The axis of saccades while converging 30 deg (assuming an equal but opposite rotation of Listing's plane) are optimal for redirecting a pseudo fovea (G′) located 30 deg temporal from the actual.

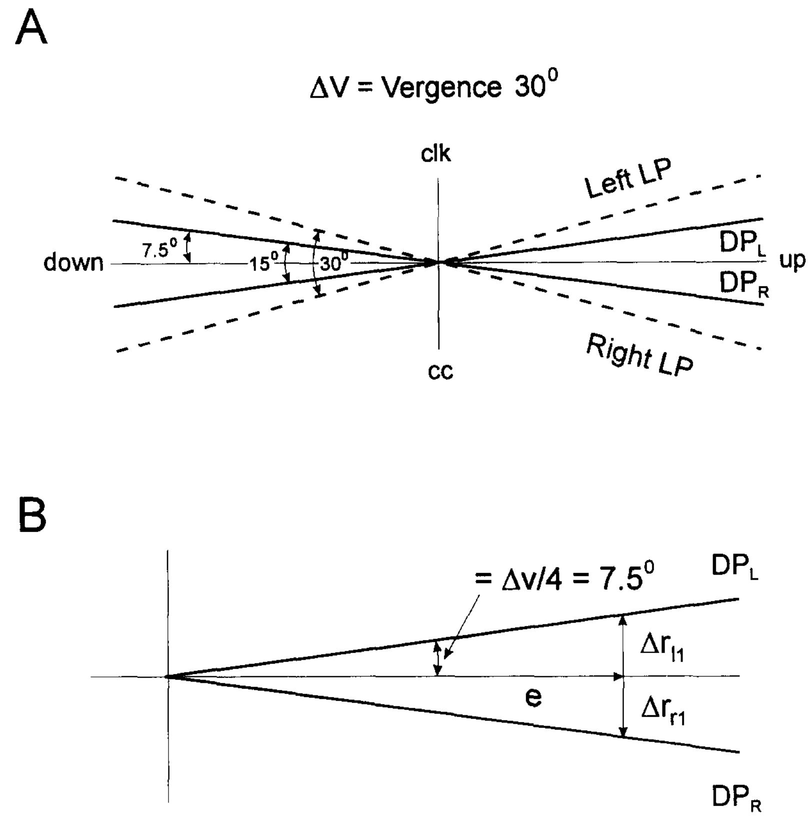

FIGURE 11. Measuring the torsional position of the eyes as a function of elevation. (A) If vergence, $\Delta v = 30$ deg, were to rotate the Listing's planes (LP) by an equal and opposite amount, the displacement planes (DP) rotate by half as far, 15 deg. (B) Shows that $\Delta r_{l1}/e = \tan(\Delta v/4)$, where e is the elevation and Δr_{l1} is the torsional component of the left eye.

when looking up. The extorsion on down gaze is consistent with the observed decrease in the tonic firing rate of superior oblique motoneurons during convergence (Mays, Zhang, Thorstad & Gamlin, 1991). With vertical prisms, the vertical vergence and primary gaze rotate in the same direction resulting in a conjugate extorsion when looking left and conjugate intorsion when looking right. The conjugate intorsion is consistent with the proposed action of the superior oblique muscle during vertical vergence (Enright, 1992). The extorsion could result from the action of the antagonist, the inferior oblique muscle. However we have no definitive functional explanation for this difference. Two possibilities follow.

(a) The position of the eye is the result of the combined signals from the vergence and saccadic systems. These signals represent rotations. The result of two consecutive rotations is dependent on the order in which they are executed; A then B is different from B then A. The fovea resetting model (Mok *et al.*, 1992) proposed that the vergence and saccadic eye position commands combine multiplicatively in the following order: saccade rotation × vergence rotation. The saccadic command is rotated by the vergence command. If vergence and conjugate saccades are represented by the quaternion vectors $\mathbf{v} = [0,0,v_3]$ and $\mathbf{s} = [0,s_2,s_3]$, the quaternion of left eye position is $\mathbf{s} \times \mathbf{v}$, then the torsional component $r_{l1} = s_2 v_3$. When the eyes are converged and looking up, then v_3 is negative and s_2 is also negative. The product r_{l1} is therefore positive, which is consistent with the fact that the left eye incyclorotates on up gaze during vergence (Fig. 11). If we change the order of composition, so that $\mathbf{r} = \mathbf{v} \times \mathbf{s}$, then $r_{l1} = -v_3 s_2$ yielding an incorrect nasal rotation of the displacement plane. The results of horizontal prism observed here could be simulated using saccade rotation × vergence rotation. Interestingly the reverse rotation of Listing's plane observed with vertical prisms could be simulated if the order of the operations were reversed, vergence rotation × saccade rotation, equivalent to rotating the vergence command by the saccadic command.

These multiplicative operation are no doubt implemented in neural circuits through a learning process. The ease with which one can fuse 30 D base-out on each eye compared to the difficulty of fusing more than a few diopters vertically suggests that this learnt circuit is not well established in the case of the latter. Thus, one explanation is that Listing's plane rotates vertically in the opposite direction from that observed with horizontal prisms because this circuit is making a mistake; it has not learnt to do these operations correctly.

(b) Another possibility is that this is not a mistake but has some underlying purpose. Van Rijn and Van den Berg (1993) have suggested that a gain of 1.0 (as defined above) for horizontal vergence produces optimal retinal correspondence. It may be that if one applies the same rule to vertical vergence as for horizontal, one does not get the same optimal retinal correspondence. To minimize torsional disparities perhaps the rules must be reversed, as observed here. Both Van Rijn and Van den Berg (1993) and Minken *et al.* (1995) have expressed vergence in terms of Helmholtz coordinates. Unlike Listing's law which uses the same half angle rule for all rotations, a Helmholtz gimbal uses different rules for horizontal and vertical rotations. It uses a vertical axis that moves with gaze imbedded in a head-fixed horizontal axis. For rotations to the left or right, the vertical axis tilts by a full angle (as much as gaze and thus more then with Listing's law) while for rotations up and down there is no tilt of the axis (thus less than the half angle rule Listing's law). Thus it may be that the vergence system rotates the eye as if it were mounted in a Helmholtz gimbal.

Finally the observation that prisms may induce a rotation of Listing's plane and thus a position-dependent torsion has important implications for the clinical use of prisms in the treatment of palsies. Because the rotation of Listing's plane is dependent on the amount of vergence (Fig. 5) it is not the prisms but the prism-induced vergence that is the important factor. This would suggest that a base-out prism used to overcome the disparity resulting from a lateral rectus palsy may result in a position-dependent torsion if the prism induced vergence. This position-dependent torsion may be of benefit to other patients such as those with torsional disparities due to palsies in the oblique muscles.

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Acknowledgements—This research was supported by the Medical Research Council of Canada grant No. MT9335. We thank L. Van Cleef for the artwork and Douglas Tweed for invaluable feedback.